

Department of Botany, Duke University, Durham, N.C., U.S.A.

Grazing preferences of two collembolan species, *Folsomia candida* and *Proisotoma minuta*, for ectomycorrhizal fungi

PEGGY ANN SCHULTZ

With 12 Figures

(Accepted: 91-03-10)

1. Introduction

Under some conditions soil invertebrate grazing can greatly reduce the beneficial effects of mycorrhizae to plants (VISSER, 1985). This study focuses on one order of common soil insects, Collembola, which maintain populations of many thousands per square meter in nearly all soils (ANDERSON & HEALEY, 1972). Studies have demonstrated that Collembola (MCMILLAN, 1976; SHAW, 1985, 1988), as well as other soil invertebrates, preferentially graze on different species of fungi (SUTHERLAND & FORTIN, 1968; MITCHELL & PARKINSON, 1976). SHAW (1985), however, was the first to show that one of the dominant collembolan species in the *Pinus contorta* (DOUGLAS) stands he studied, *Onychiurus armatus* (TULLBERG), differentially grazed saprophytic and ectomycorrhizal fungi.

Little work has been done to examine the effects of collembolan grazing on mycorrhizae, but two studies have shown they can significantly reduce the growth rates of mycorrhizal plants. WARNOCK *et al.* (1982) and FINLAY (1985) reported the growth rates of endomycorrhizal leeks, *Allium porrum* (L), and clover, *Trifolium pratense* L. respectively, in greenhouse experiments were greatly reduced when *Folsomia candida* (WILLEM) were present at high number densities. WARNOCK *et al.* postulated (1982) that insect grazing on external mycelia of fungi reduces the capacity of the fungi to transport nutrients.

The present study was conducted to determine if two species of Collembola, *F. candida* and *Proisotoma minuta* (TULLBERG) graze preferentially on ectomycorrhizal fungi. The results are of interest due to the potential impact of hyphal grazing on host plant nutrition.

2. Materials and methods

2.1. Culture of Collembola and fungi

F. candida was isolated from a soybean field in Illinois, and *P. minuta* was isolated from a pine forest at the University of Michigan Biological Station. These species were used because they have been used in other grazing experiments (WARNOCK *et al.*, 1982; FINLAY, 1985; MOORE *et al.*, 1985), and because they are amenable to laboratory culture. The insects were bred in sealed culture jars on a substrate composed of a 2:1:1 mixture of plaster of Paris, activated charcoal and water. The substrate was air dried for a minimum of three days prior to insect colonization as suggested by USHER and STONEMAN (1977). Insect cultures were incubated at 19–22 °C with relative humidities greater than 90%. The Collembola were fed on a diet of baker's yeast preceding the experiments.

All ectomycorrhizal fungi (table 1) were transferred from stocks onto M-40 medium (STEVENS, 1974) with the exception of *Leccinum scabrum* cultures used in experiments 2 and 3, which was grown on potato dextrose agar (PDA) (STEVENS, 1974) as suggested by TRAPPE (pers. comm. 1988). The

concentration of agar used for both the M-40 and PDA plates was 3.0%. After inoculation, the plates were sealed with parafilm and incubated at 22 °C for approximately one month prior to starting the experiments.

2.2. Experimental chambers

The experimental chambers were constructed by placing four aluminium discs, 10 mm in diameter, equidistant along the outer portion of 50 mm petri dishes and then pouring into these dishes a 2:1:1 mixture of plaster of Paris, activated charcoal and water. After the mixture solidified, the aluminium discs were removed, creating wells into which non-inoculated plugs of nutrient agar and plugs of nutrient agar colonized by fungi could be inserted (LEONARD, 1984; MOORE *et al.*, 1987; WALTER *et al.*, 1986).

Table 1. Fungi used in Experiment 1 within their respective family groups are listed below.

		Isolate number
Agaricales		
Agaricaceae		
<i>Hebeloma crustuliniforme</i> (BULL. ex ST. AM.) QUEL.		S-166
<i>Laccaria laccata</i> (SCOP. ex FR.) BERK and BR.		S-447
<i>Paxillus involutus</i> (BATSCH ex FR.) FR.		403
Boletaceae		
<i>Leccinum scabrum</i> (BULL. ex FR.) S. F. GRAY		524
<i>Suillus albipes</i> (PECK) SINGER		6361
<i>Suillus cavipes</i> (Opat.) SMITH et THIERS		S-298
<i>Suillus tomentosus</i> (KAUFFM.) SINGER, SNELL et DICK		7644
Thelophorales		
Thelophoraceae		
<i>Thelephora terrestris</i> (EHRH.) FR.		S-142
Hymenogastrales		
Rhizopogonaceae		
<i>Rhizopogon fuscorubens</i> A. H. SMITH		7993
<i>Rhizopogon hawkerii</i> A. H. SMITH		7433
<i>Rhizopogon rubescens</i> (TUL.) TULASNE		648
<i>Rhizopogon smithii</i> HOSFORD		81329
Melanogastraceae		
<i>Alpova olivaceotinctus</i> (A. H. SMITH) [in SMITH and ZELLER] TRAPPE		8245
<i>Melanogaster tuberiformis</i> CORDA [in Sturm]		7679
Gautieriaceae		
<i>Gautieria otthii</i> TROG		6362

All isolates were obtained from Dr. RANDY MOLINA, USDA, Forest Service, Forestry Science Laboratory, Corvallis OR.

2.3. Experiment 1

A 4×4 balanced lattice design (COCHRAN & COX, 1957) was used to arrange the sixteen choices (fifteen fungi and uninoculated nutrient agar control) so that they could be ranked with respect to insect preference. The sixteen choices were compared four at a time (four per experimental chamber) in all possible combinations requiring twenty experimental chambers.

After the fungi and the control plugs were placed in the experimental chambers, twenty adult insects (body length ≥ 2.0 mm) were immobilized using CO_2 and added to each chamber. The positions of insects relative to the agar plugs were recorded over the course of two and a half days at 6 to 8 hr

intervals. All insects observed were counted and their distribution recorded on the basis of being associated with any of the four plugs (within 2 mm diameter of the plug) or not being associated with any of the plugs.

The proportion of insects that visited the four plugs in each chamber was determined and then the proportions associated with the five replicates of each of the sixteen choices were summed. The proportions associated with the sixteen choices were arcsine transformed and a 2 way analysis of variance (ANOVA) was performed using SAS. The independent variables were the experimental chambers and the fungi/uninoculated nutrient agar control. The dependent variable was the arcsin transformed proportion of insects associated with each choice. Because the variance between choices was significantly greater than the variance within individual choices ($p = 0.05$) the 2-way ANOVA was followed by a Tukey test for multiple comparisons.

2.4. Experiments 2 and 3

Four fungi, *L. scabrum*, *Gautieria otthii*, *Alpova olivaceotinctus*, and *Melanogaster tuberiformis* were chosen from the original fifteen and pairwise compared in every possible combination in Experiments 2 and 3. *L. scabrum* and *M. tuberiformis*, were used to confirm they were grazed differentially by *F. candida*. The other fungi were used to determine if trends in *F. candida* preference observed in Experiment 1 (fig. 1) would be significant if the variability were reduced and the number of replicates increased. My reasons for choosing *G. otthii* and *A. olivaceotinctus* were somewhat arbitrary but based in part on how quickly they grew in culture. New chambers were made for the second and third experiment but the design of the experimental chambers was the same as in Experiment 1. Included in each chamber were two inoculated plugs and two uninoculated control plugs, M-40 and PDA. Twenty adult *F. candida* were added to each experimental chamber and their positions recorded as indicated below. Each of the six pairwise comparisons was replicated four times.

Experiment 3 was designed to determine whether a second collembolan species, *P. minuta*, exhibited the same grazing preferences as *F. candida* for the four fungi compared in experiment 2. *P. minuta* is smaller than *F. candida*, individuals are less than 2 mm in length at maturity, a dissecting scope was used to monitor their positions. Roughly 100 individuals

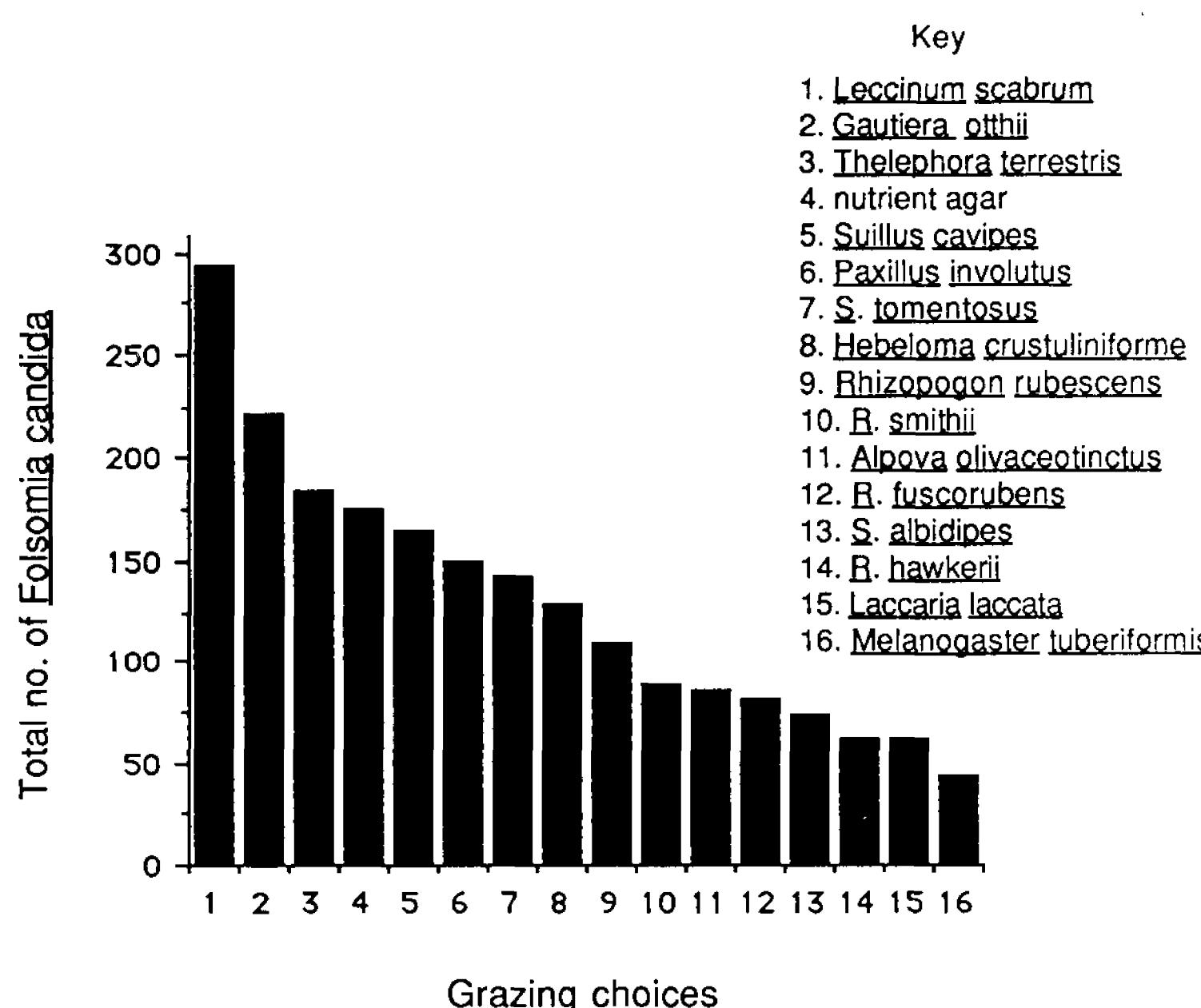


Fig. 1. Experiment 1, total number of *Folsomia candida* on the sixteen differently grazing choices. Only 1 and 16 were visited significantly differently by *F. candida*.

were added to the experimental chambers. The four replicates of *L. scabrum* & *M. tuberiformis*, *L. scabrum* & *A. olivaceotinctus* and *A. olivaceotinctus* & *M. tuberiformis* for both the *F. candida* and *P. minuta* species were run simultaneously. *F. candida* and *P. minuta* positions were recorded at the same times for as long as *P. minuta* positions were recorded. *P. minuta* and *F. candida* positions were recorded 2.5, 5 and 8 hrs after the experiment was begun. *F. candida* positions were additionally recorded 10.5, 19, 20.5, and 28.5 hrs after the experiments were begun. The remaining comparisons were begun three weeks later. Because *P. minuta* removed all the hyphae from the surface of the agar of the preferred fungi very quickly on the first date, insects were counted more frequently on the second date. *P. minuta* and *F. candida* positions were recorded at 2.5, 4, 6.5, 9.5 and 18 hrs after the insects were added to the experimental chambers; *F. candida* positions continued to be recorded 22, 24.5, and 27.5 hrs after the experiments were begun.

The data from experiments 2 and 3 were analyzed using profile analysis for repeated measures, using Systat software. When there were significant differences in the insect distribution on the plugs two hypotheses were tested. One test compared the differences in insect numbers between the fungal choices. The other test compared the differences between the fungal choices and the uninoculated controls of PDA and M-40. Three different multivariate F statistics were run on the matrices: the Wilks lambda; the Pillai trace and the Hotelling-Lawley trace (WILKINSON, 1987; WINER, 1971). If these F-statistics differed, the most conservative value was reported.

To verify that the insects were feeding on fungi, insects were killed in 90% ethanol, cleared in lactophenol overnight and mounted on microscope slides using Hoyer's medium. The gut contents of 5 *F. candida* from the first experiment and 10–15 *P. minuta* from three comparisons were scanned for the presence of fungal hyphae using phase contrast illumination.

To determine if collembolan preference was related to the hyphal diameter of the four fungal species used in the second and third experiments hyphae of each species were measured. Hyphae from the cultures used in the choice experiments were removed one to three weeks after the experiments were completed and the diameter of 5 aerial hyphae of each of the four fungal species measured using phase contrast illumination (1000X). A student T-test was performed on these data.

3. Results

3.1. Experiment 1

The data from the first experiment were analyzed using a 2-way ANOVA, time and choice were the two variables. The means of the 15 fungi and uninoculated nutrient agar control were significantly different ($p \leq 0.04$). Insects visited all choices (fig. 1) but only the difference between *L. scabrum*, the most visited fungus, and *M. tuberiformis*, the least visited fungus was significant ($p \leq 0.05$). Insect choice was not significantly different across experimental chambers ($p \leq 0.994$).

The positions of *F. candida* generally reflected grazing preference. Insects were observed grazing on the choices visited as indicated by the disappearance of the aerial and submerged hyphae of the preferred fungi, while the hyphae of the less preferred fungi remained intact.

3.2. Results for experiments 2 and 3

F. candida preferred *G. otthii* over *L. scabrum*, *M. tuberiformis* and *A. olivaceotinctus* (figures 2, 3, 4 and table 2). The overall differences between the choices in these comparisons

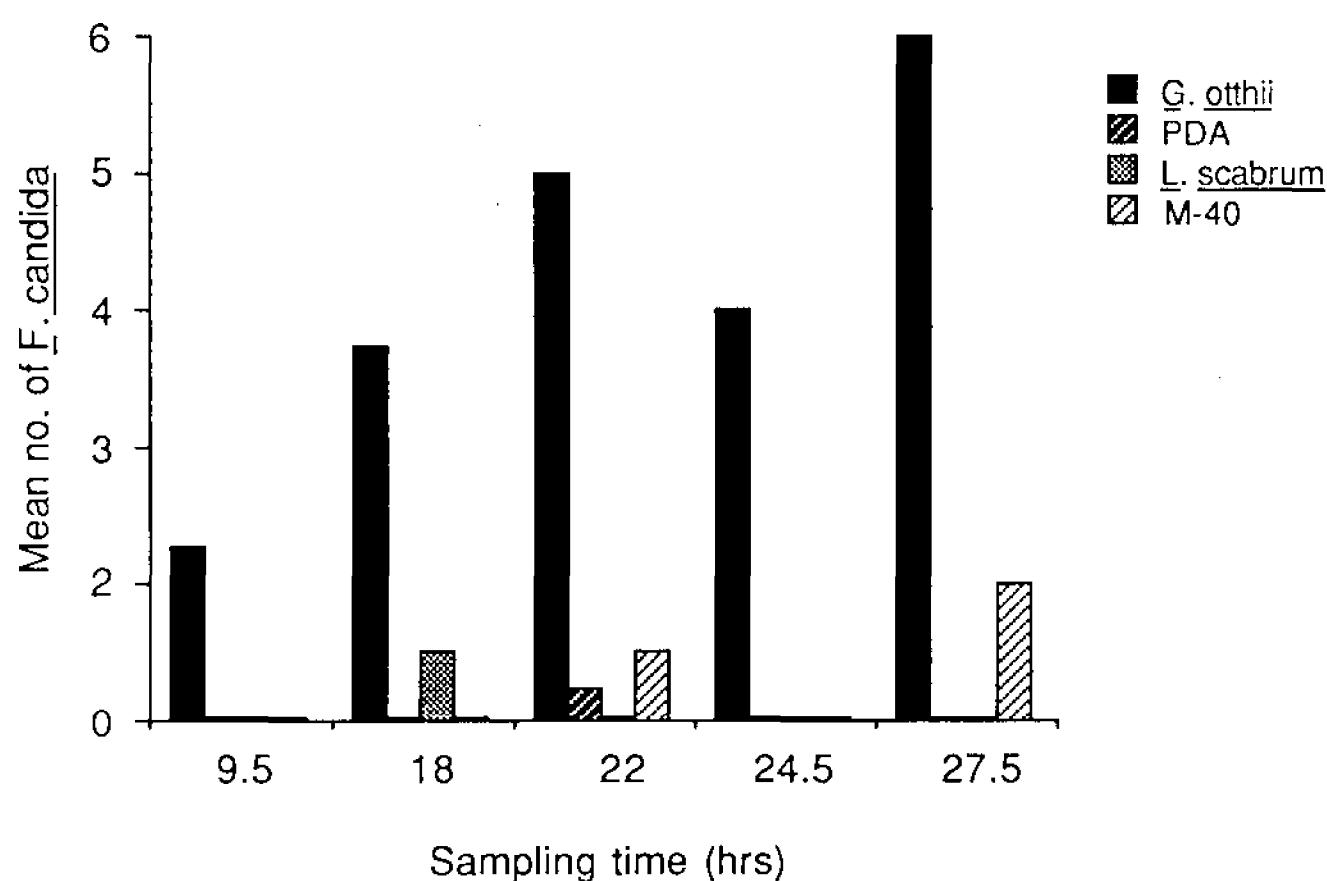


Fig. 2. Experiment 2, mean number of *Folsomia candida* on the pairwise comparisons of the four replicates of *Gautieria otthii* and *Leccinum scabrum*.

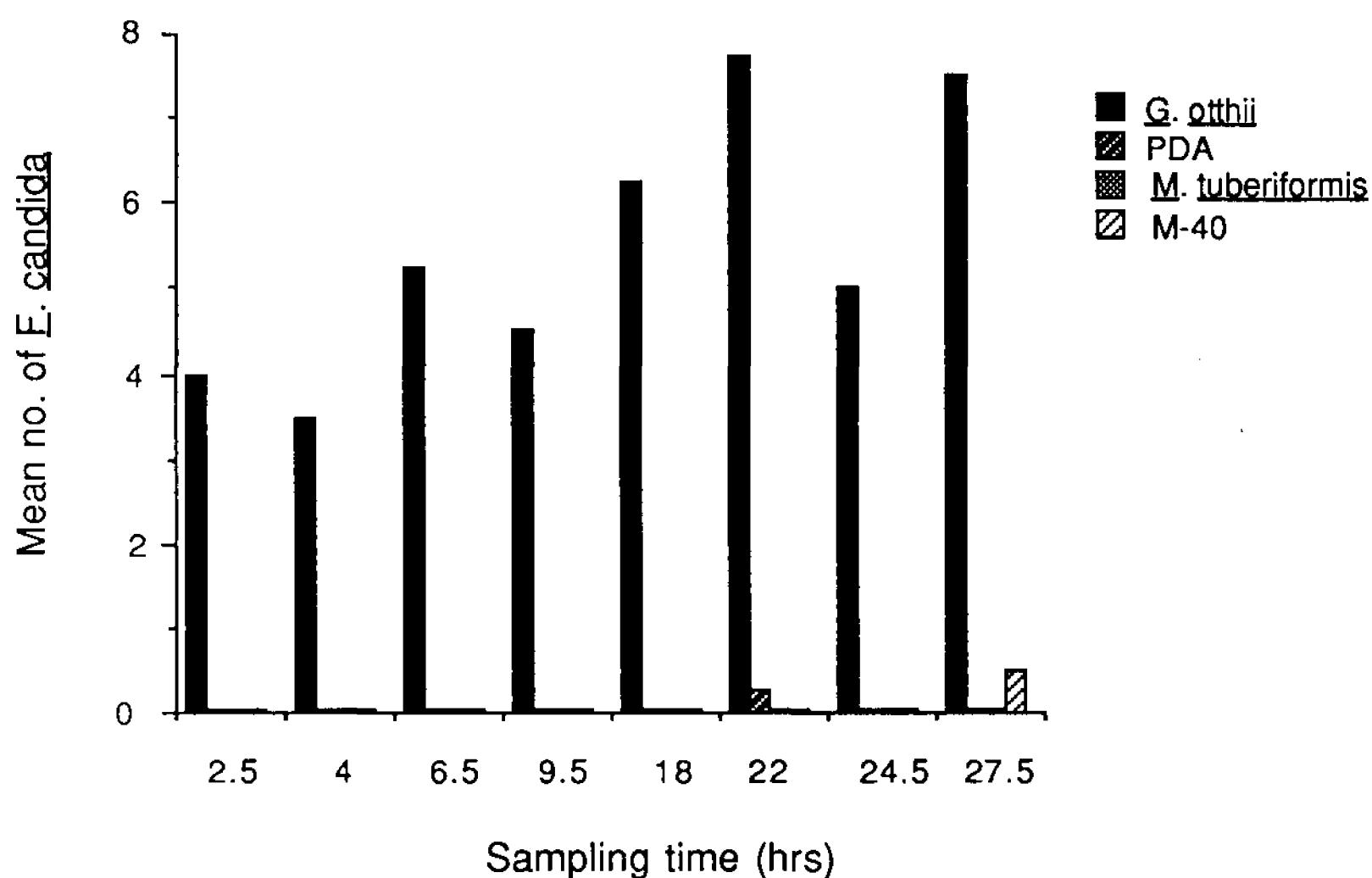


Fig. 3. Experiment 2, mean number of *Folsomia candida* on the plugs of the four replicates of the pairwise comparisons between *Gautieria otthii* and *Melanogaster tuberiformis*.

were significant ($p \leq 0.001$). In the comparison between *G. otthii* and *A. olivaceotinctus* the overall difference was significant ($p \leq 0.001$). Similarly a significantly greater number of insects were on the fungi *versus* the control plugs. The insects preferred *G. otthii* so strongly when compared to *L. scabrum* and *M. tuberiformis* that Systat would not run the statistics for the profile analysis because there was no variance at several sampling times, all the insects that made a choice were on or near *G. otthii*.

F. candida preferred the PDA and M-40 controls over *M. tuberiformis* and *A. olivaceotinctus* ($p = 0.01$). There were no significant differences in the numbers of insects visiting M-40 or PDA plugs ($p = 0.8$) (Figure 5).

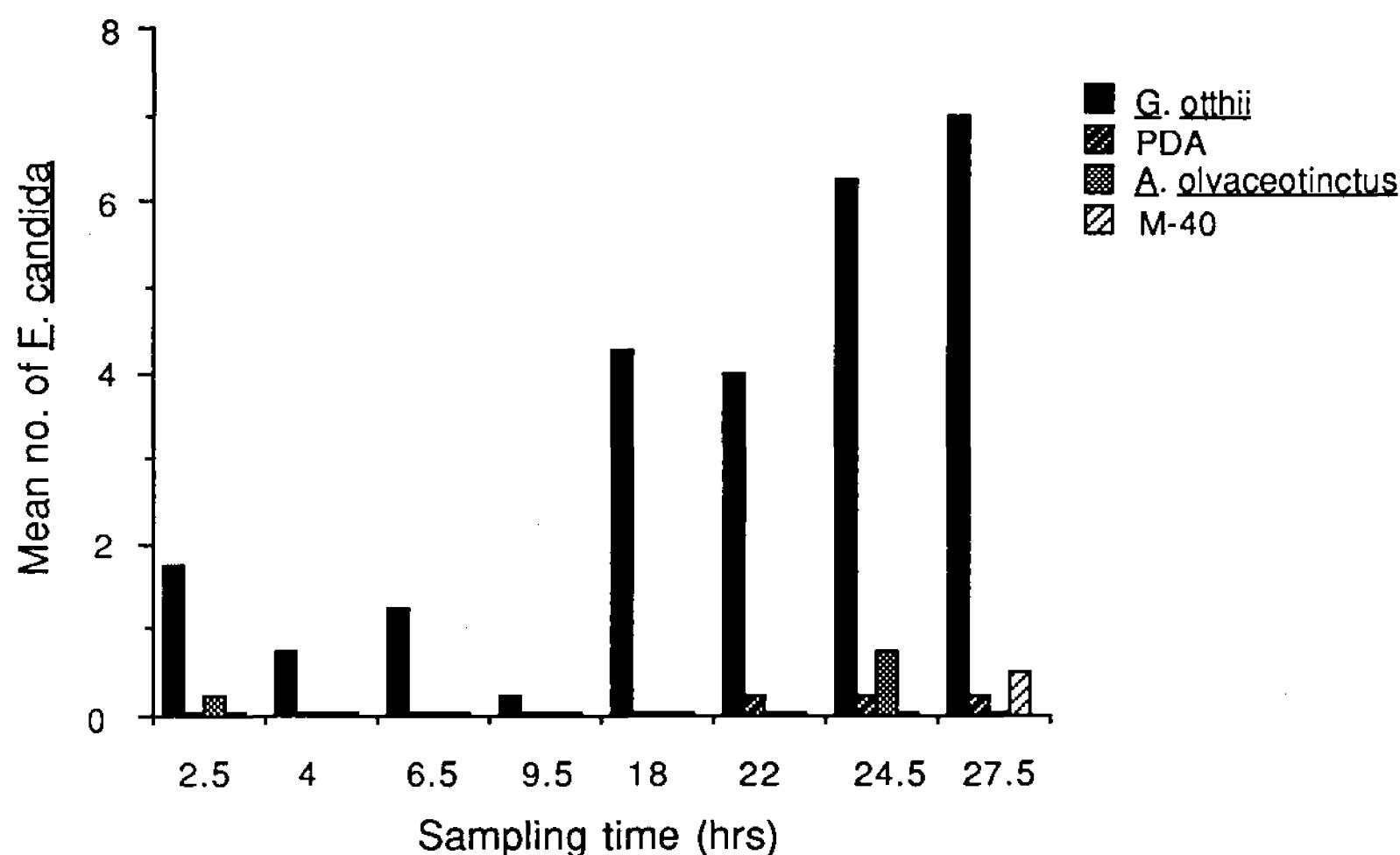


Fig. 4. Experiment 2, mean number of *Folsomia candida* from the four replicates of the pairwise comparisons between *Gautieria otthii* and *Alpova olivaceotinctus*.

Table 2. The significance levels of the overall differences between fungi and controls; the differences between the fungi and the differences between the fungi and controls for each comparison in experiments 2 and 3 are shown below

Comparison	overall difference	difference between fungi	difference between fungi and control
<i>Folsomia candida</i>			
<i>G. otthii</i> & <i>L. scabrum</i>	p = 0	p = 0	p = 0
<i>G. otthii</i> & <i>M. tuberiformis</i>	p = 0.001	no variance	no variance
<i>G. otthii</i> & <i>A. olivaceotinctus</i>	p = 0	p = 0	p = 0
<i>M. tuberiformis</i> & <i>A. olivaceotinctus</i>	p = 0.001	p = 0.8	p = 0.01
<i>L. scabrum</i> & <i>A. olivaceotinctus</i>	p = 0.289	no variance	no variance
<i>L. scabrum</i> & <i>M. tuberiformis</i>	p = 0.001	p = 0.02	p = 0.07
<i>Proisotoma minuta</i>			
<i>G. otthii</i> & <i>L. scabrum</i>	p = 0	p = 0	p = 0.02
<i>G. otthii</i> & <i>M. tuberiformis</i>	p = 0.002	p = 0	p = 0.01
<i>G. otthii</i> & <i>A. olivaceotinctus</i>	p = 0	p = 0	p = 0.03
<i>M. tuberiformis</i> & <i>A. olivaceotinctus</i>	p = 0	p = 0.88	p = 0
<i>L. scabrum</i> & <i>A. olivaceotinctus</i>	p = 0	p = 0	p = 0.21
<i>L. scabrum</i> & <i>M. tuberiformis</i>	p = 0.008	p = 0	p = 0.02

F. candida preferred *L. scabrum* over *M. tuberiformis* ($p = 0.002$). However, when the fungi were compared to the control plugs there was no significant difference between them ($p = 0.07$) (Figure 6). *L. scabrum* was not visited significantly more often than *A. olivaceotinctus*. There were no significant differences between the fungi, nor were there significant differences between the fungi and the controls. The insects did not visit any of the choices offered.

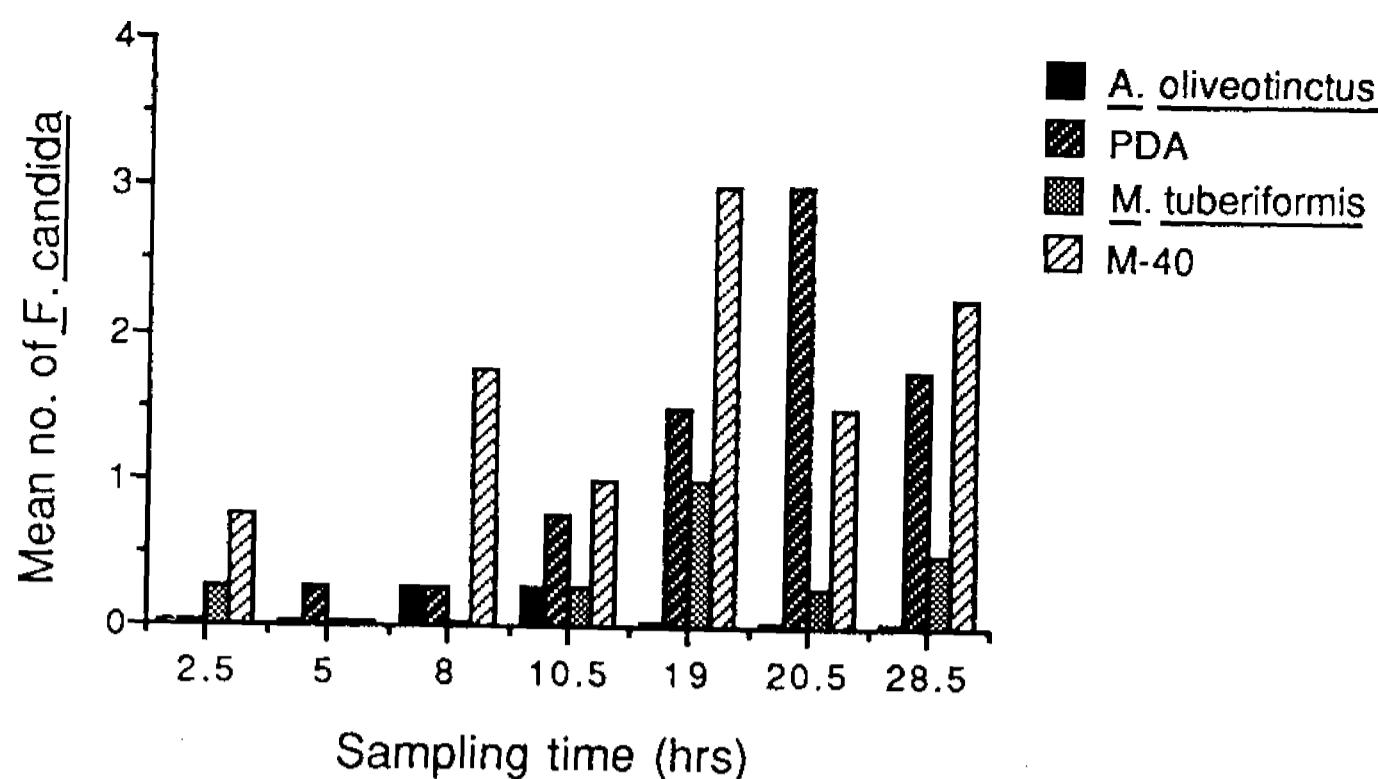


Fig. 5. Experiment 2, mean number of *Folsomia candida* from the four replicates of the pairwise comparisons between *Melanogaster tuberiformis* and *Alpova olivaceotinctus*.

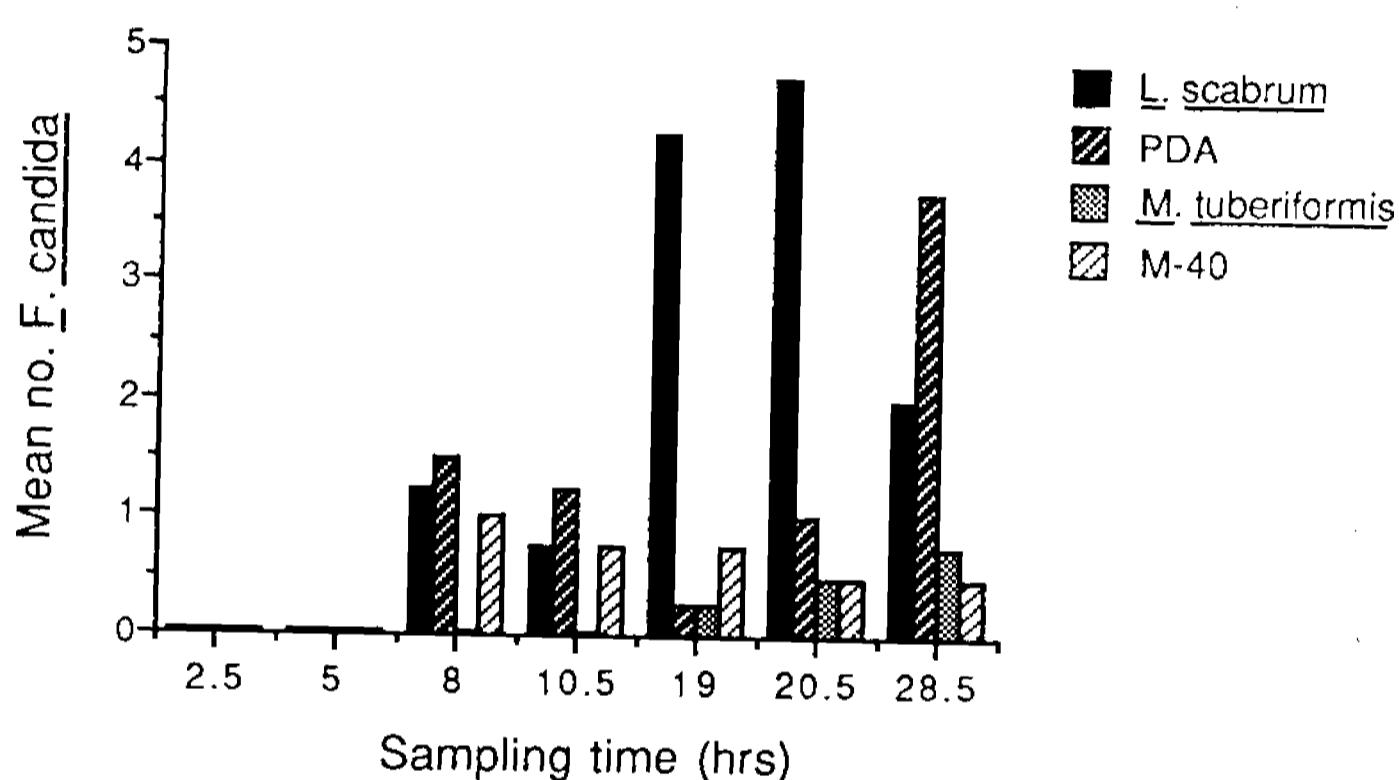


Fig. 6. Experiment 2, mean number of *Folsomia candida* from the four replicates of the pairwise comparisons between *Leccinum scabrum* and *Melanogaster tuberiformis*.

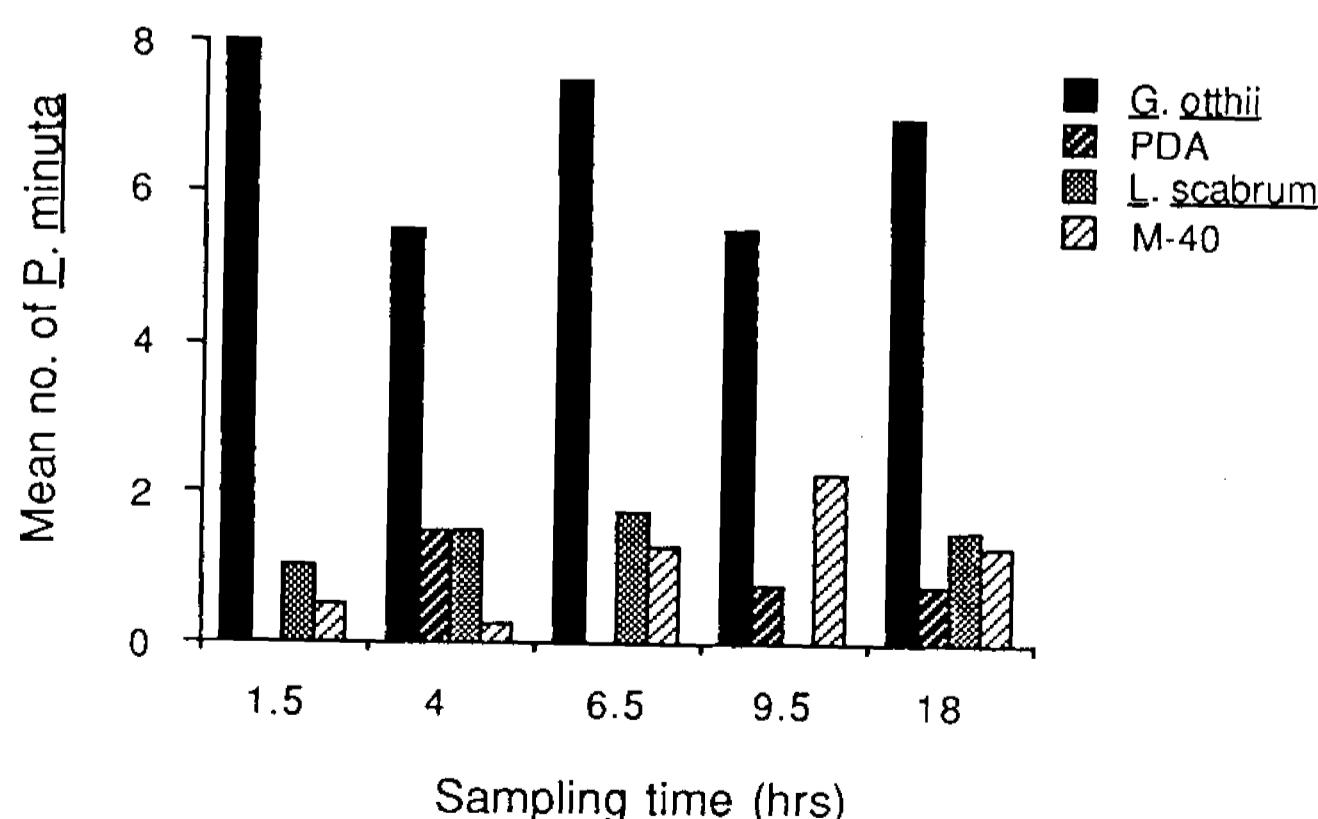


Fig. 7. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Gautieria otthii* and *Leccinum scabrum*.

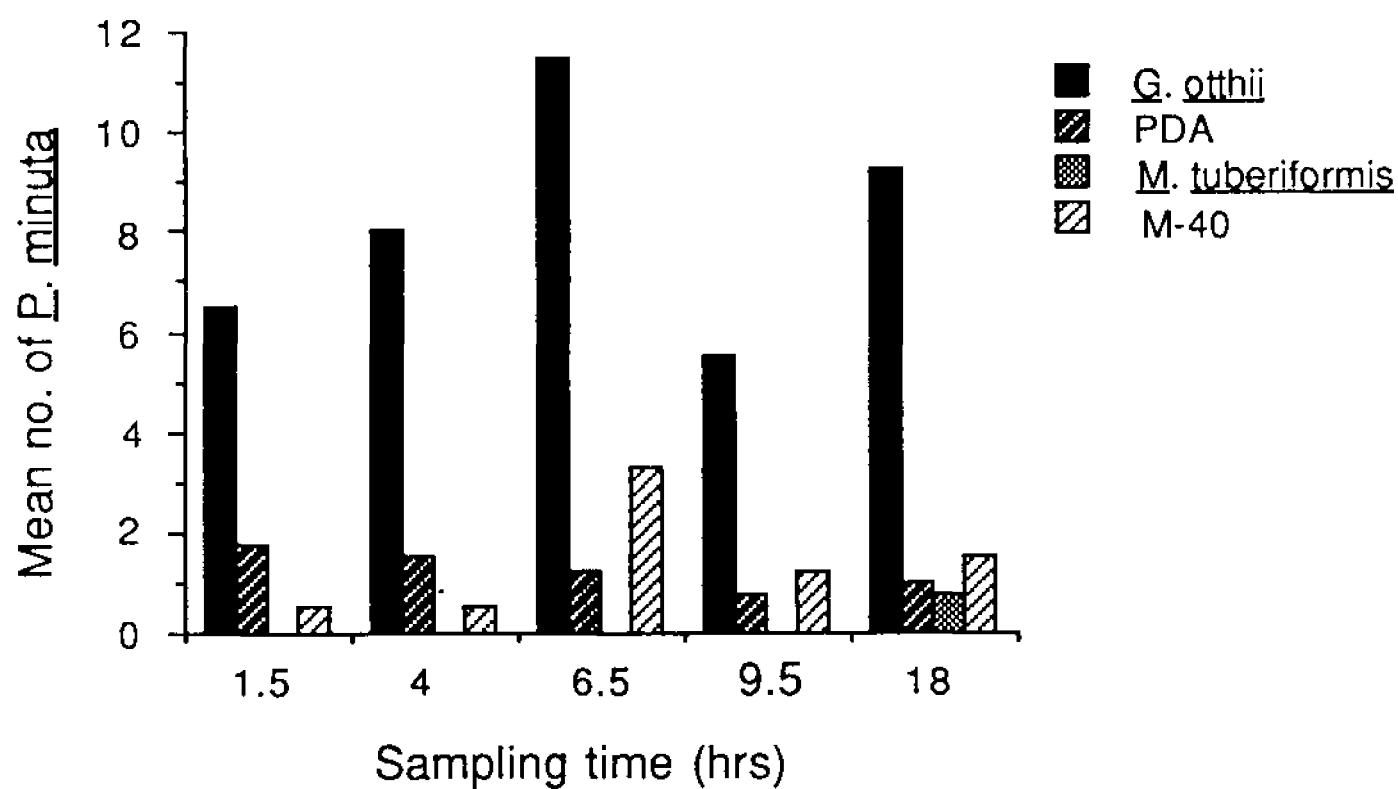


Fig. 8. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Gautieria otthii* and *Melanogaster tuberiformis*.

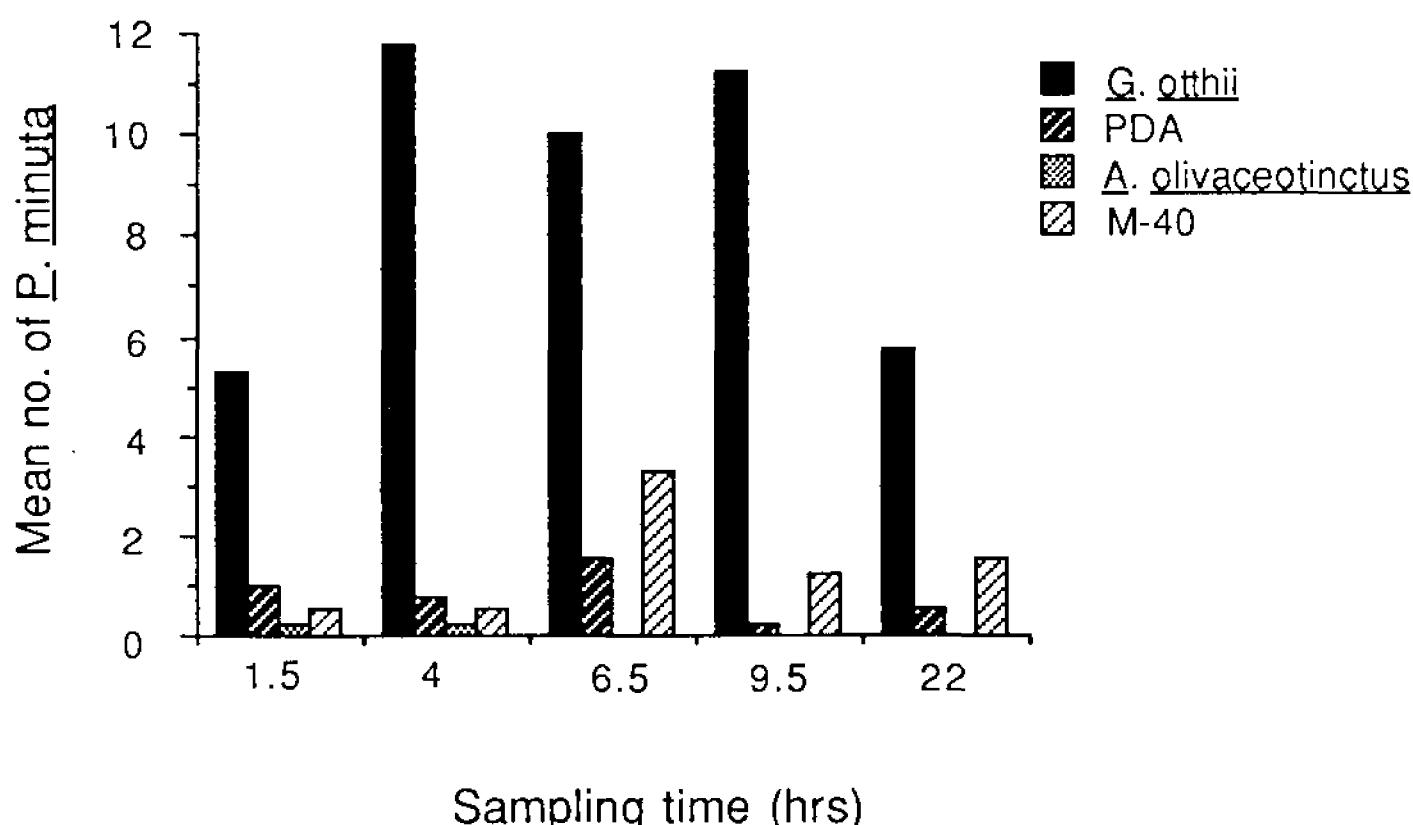


Fig. 9. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Gautieria otthii* and *Alpova olivaceotinctus*.

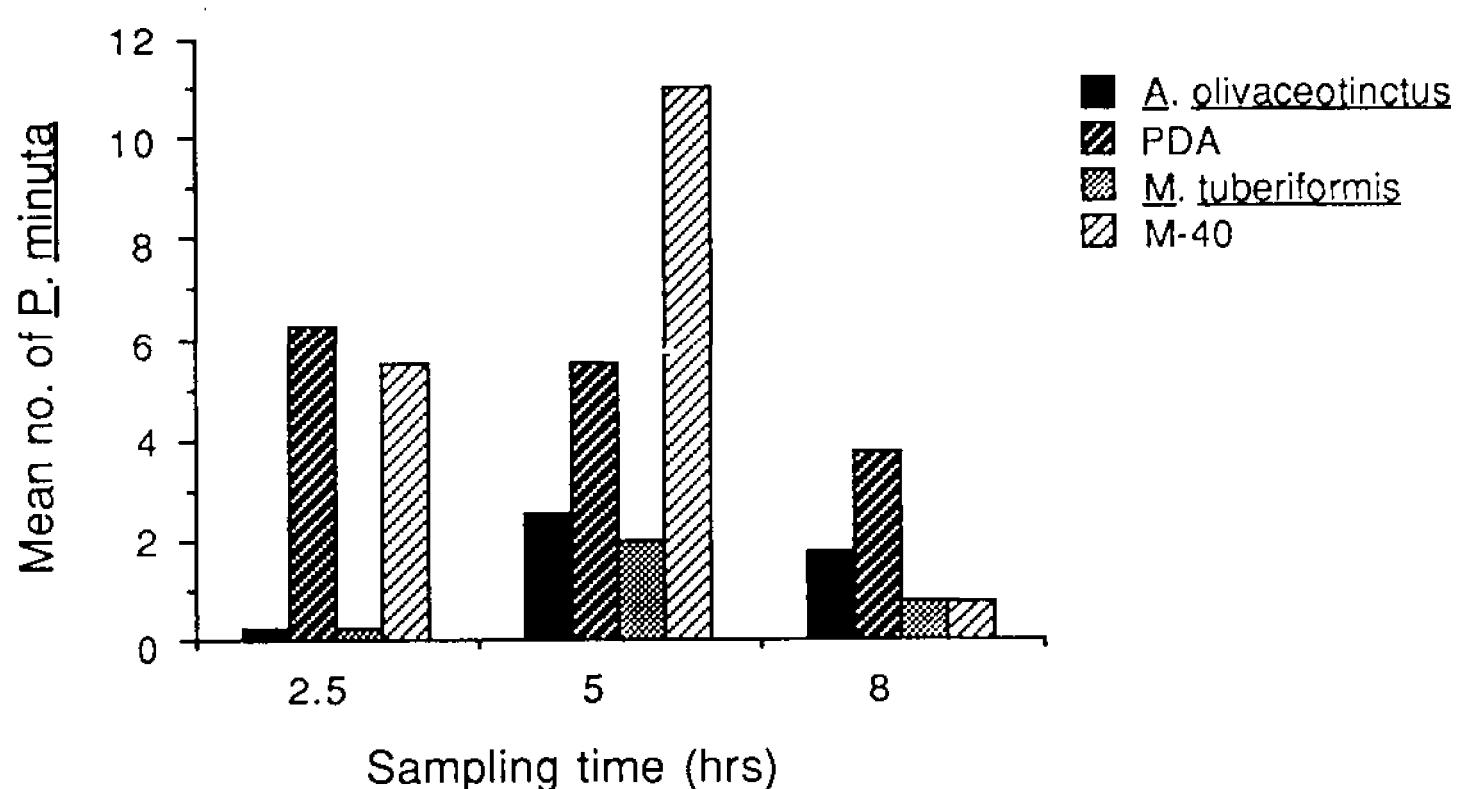


Fig. 10. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Melanogaster tuberiformis* and *Alpova olivaceotinctus*.

P. minuta preferences were almost identical to *F. candida*. Like *F. candida*, *P. minuta* differentially visited the choices in all six comparisons ($p \leq 0.008$). *P. minuta* preferred *G. otthii* over *L. scabrum*, *M. tuberiformis* and *A. olivaceotinctus* ($p = 0$). In these three comparisons there were significantly more insects visited the fungi compared to the controls ($p \leq 0.03$) (figures 7, 8 & 9).

Like *F. candida*, *P. minuta* preferred the controls over *M. tuberiformis* and *A. olivaceotinctus* ($p = 0$). There were no significant differences in the numbers of insects that visited the two fungal plugs ($p = 0.88$) (figure 10).

P. minuta preferred *L. scabrum* over *M. tuberiformis* and *A. olivaceotinctus* ($p = 0$) (figures 11 & 12). While *P. minuta* preferred the fungi over the controls in the *L. scabrum* and *M. tuberiformis* comparison ($p = 0.02$), differences in between the fungi and the controls were not significant in the *L. scabrum* and *A. olivaceotinctus* comparisons.

Both *F. candida* and the *P. minuta* ate hyphae. The gut contents of 5 *F. candida* taken from a pooled sample of the insects from the first experiment contained hyphae. The gut contents of 13 *P. minuta* from the *L. scabrum*-*A. olivaceotinctus* comparison were examined:

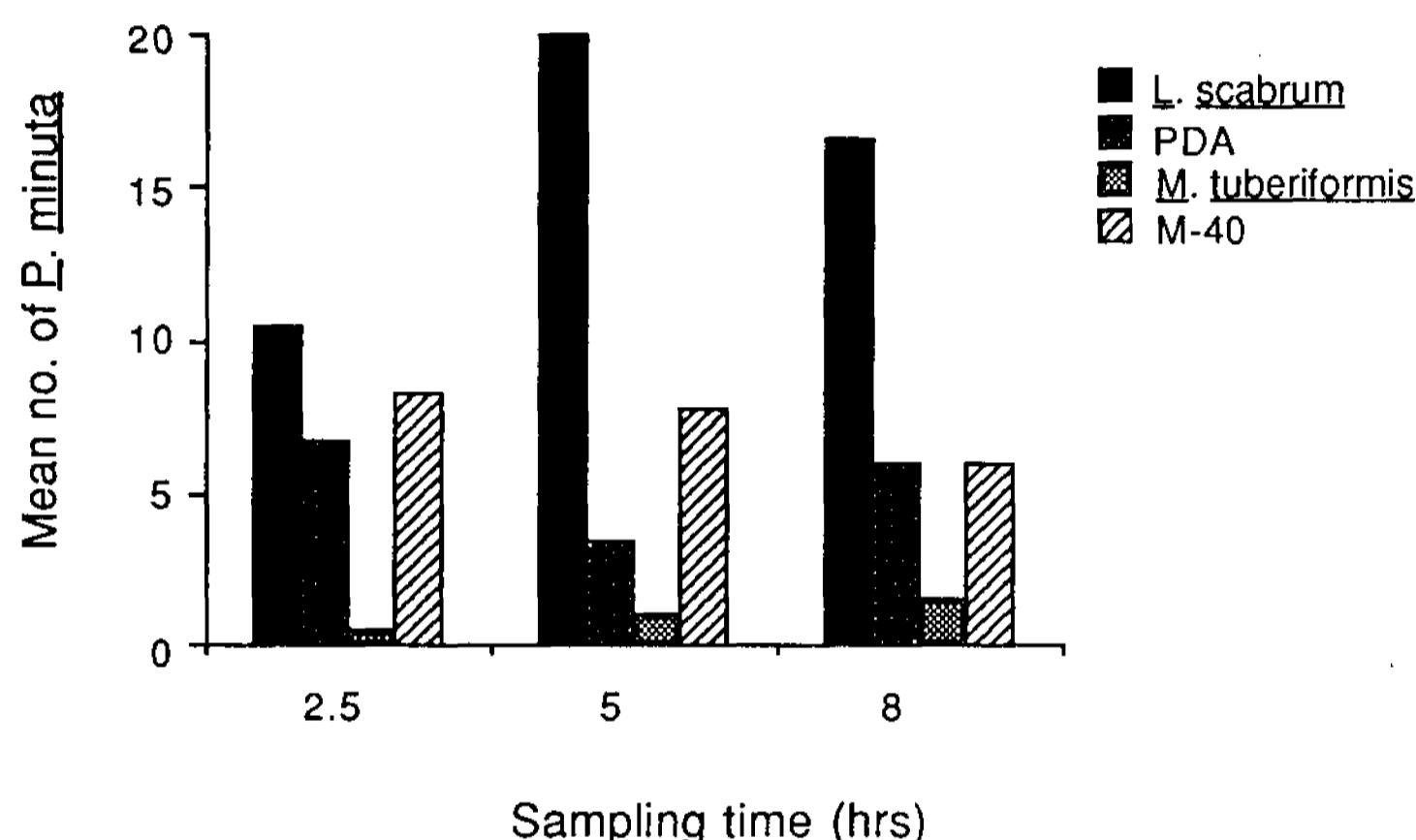


Fig. 11. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Leccinum scabrum* and *Melanogaster tuberiformis*.

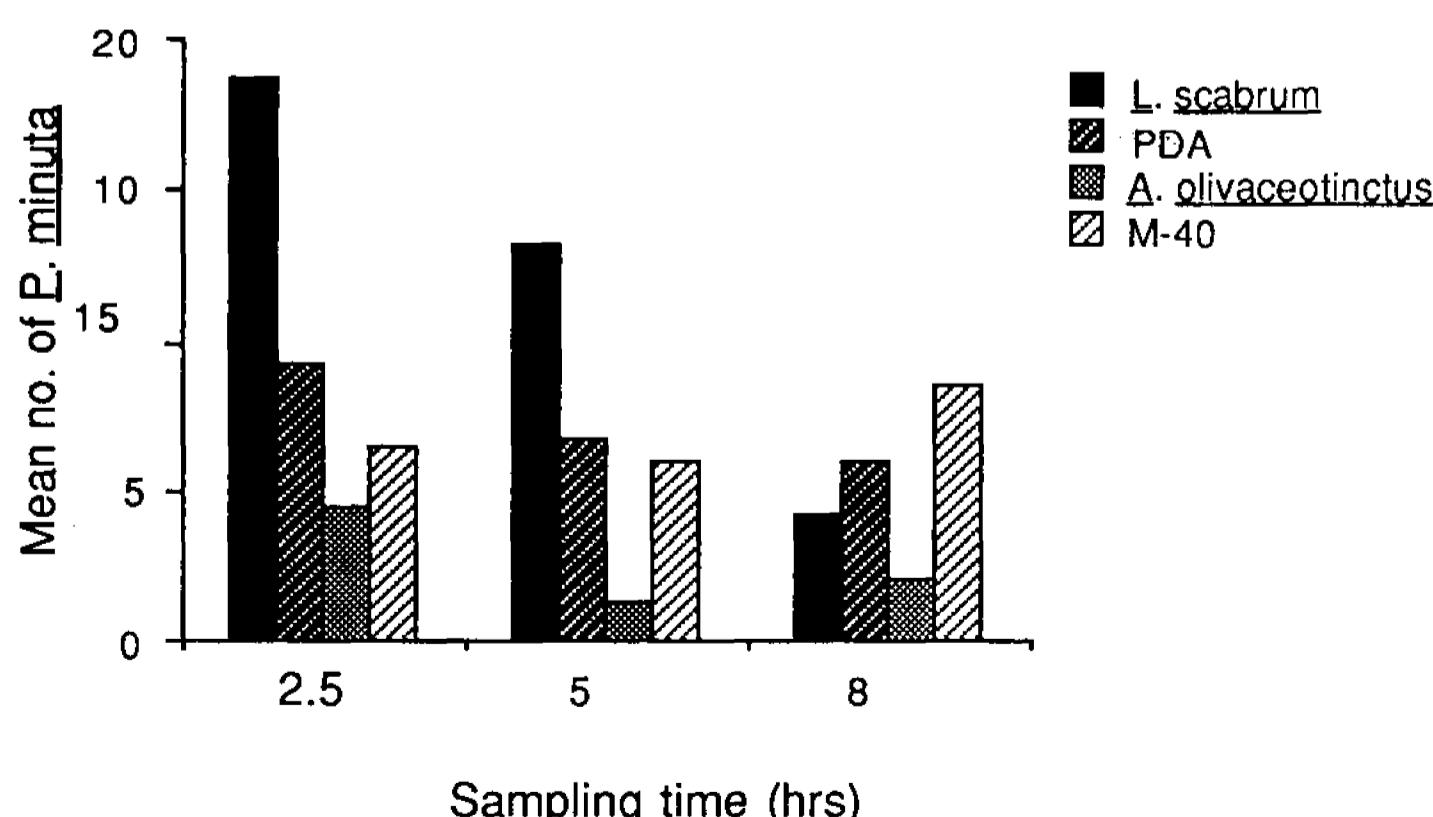


Fig. 12. Experiment 3, mean number of *Proisotoma minuta* from the four replicates of the pairwise comparisons between *Leccinum scabrum* and *Alpova olivaceotinctus*.

7 had hyphae in their guts, 1 did not have hyphae in its gut and the remaining insects had undeterminable debris in their guts. Fifteen *P. minuta* from the *L. scabrum*-*M. tuberiformis* comparison were examined: 7 had hyphae in their guts, 5 had no hyphae in their guts and 3 were not clear enough to determine. The gut contents from 10 *P. minuta* taken from the *M. tuberiformis*-*A. olivaceotinctus* comparison were examined: one clearly had hyphae in its guts, the remaining had no hyphae in their guts. Some guts were full of hyphae, some had smaller amounts of hyphae, others appeared to be empty, many were very dark due to the presence of charcoal; many guts contained what appeared to be agar along with the charcoal and hyphae.

The differences between the hyphal diameters of the four fungi used in Experiments 2 and 3 were not significant ($p \geq 0.05$). *L. scabrum* hyphae ranged from 3.5 to 4.5 μm in diameter, *G. otthii* 0.9 to 1.3 μm , *M. tuberiformis* 2.6 to 4.4 μm and *A. olivaceotinctus* 1.8 to 2.6 μm .

4. Discussion

Collembola are generalists, grazing on a wide range of soil microorganisms. McMILLAN (1976) showed that *O. armatus* grazed on a wide range of species of fungi, yeast and bacteria. SHAW (1985, 1988) found that *O. armatus* grazed on many ectomycorrhizal and saprophytic fungi. In this study *F. candida* visited and probably grazed many different species of ectomycorrhizal fungi. However, in all these studies the insects preferentially grazed some subset of the food choices presented.

In the second and third experiments *F. candida* preferred *L. scabrum* over *M. tuberiformis* and *P. minuta* preferred *L. scabrum* over *A. olivaceotinctus* but in these comparisons where there was no significant difference between the fungi and the controls. Because *M. tuberiformis* was visited less than or equal to the control plugs, in the comparison between *L. scabrum* and *M. tuberiformis*, there was no significant difference between the fungal and control plugs even though insects visited *L. scabrum* much more often than the other choices. By the last sampling time in the *L. scabrum*-*A. olivaceotinctus* comparison all the aerial hyphae in at least two of the replicates had been removed from *L. scabrum* plugs by *P. minuta*. There were no more insects on the *L. scabrum* than the control plugs at this sampling time. Given that at one of the three sampling times there was no difference between the controls and the preferred fungal plugs, it is not surprising there was no significant difference between the fungal and control plugs.

F. candida and *P. minuta* responded differently to the stress of being placed in the experimental chambers and the disturbance they were subjected to each time they were sampled. *F. candida* usually required at least 8 hrs to acclimate to the experimental chambers enough to begin to feed. In the comparison between *L. scabrum* and *A. olivaceotinctus*, *F. candida* never became acclimated enough to feed, the insects remained clustered in the center or lined the periphery of the experimental chambers, shed ectoskeletons and eggs were seen in the experimental chambers. *P. minuta*, however, acclimated very quickly to the experimental chambers, usually they were feeding a couple hours after being placed in the chambers. Although a dissecting microscope and a light were used when *P. minuta* was counted they often were not affected by the change in light. *F. candida*, on the other hand, launched across the experimental chambers if I breathed too closely to the chamber. Although *F. candida* was more sensitive to changes in the environment this did not appear to influence their grazing choices. They were usually back to the preferred choices a few hours after being disturbed.

Insects could prefer certain fungi for morphological reasons such as hyphal diameter, or cell wall thickness. Initially, I thought hyphal diameters might affect insect choice. However, there were no significant differences in hyphal diameter between the fungi in the second experiment. The cell walls of the fungi used in the second and third experiment were

less than one micrometer, therefore it is unlikely that the cell wall thickness influenced collembolan grazing.

Familiarity with the food choice probably did not affect grazing choice in this study since both *F. candida* and *P. minuta* were reared in culture and fed Baker's yeast for at least six months prior to the experiments. Therefore, grazing choice was determined by some property of the fungi.

Insect preference could be related to the toxic properties of the fungi or the nutrient quality of the fungi (MOORE *et al.*, 1985). *F. candida* and *P. minuta*'s avoidance of *A. olivaceotinctus* and *M. tuberiformis* suggest these fungi have toxic properties. When *P. minuta* was placed in experimental chambers with the two least preferred fungi and the controls, both of the controls had significantly higher numbers of insects associated with them than the fungal plugs. Additionally, after *P. minuta* removed the aerial hyphae of the more preferred choices it did not move to the agar plugs containing *A. olivaceotinctus* or *M. tuberiformis*, rather the insects moved onto the control plugs. The shift to control plugs was not observed in Experiment 1, probably because *F. candida* did not completely remove the aerial hyphae of the most preferred choices. Finally, insects recorded as associated with either of the least preferred fungi were often moving across the hyphae while insects associated with the preferred choices were often stationary and feeding on hyphae.

The differences in grazing between the more preferred fungi and least preferred fungi are better explained by the least preferred fungi having toxic properties. The differences between the more preferred fungi, however, are best explained by differences in nutrient quality since both *G. otthii* and *L. scabrum* were grazed but to varying degrees when *F. candida* and *P. minuta* could choose between them.

The position of insects within the experimental chambers appears to be based primarily on the location of food. While past and current position of other collembolans may cause collembola to aggregate at high densities (LEONARD & BRADBURY, 1984; USHER & HIDER, 1975) I do not believe that aggregation affected the results of this experiment. In a preliminary study of *F. candida* grazing patterns, insects tended to distribute themselves among four food sources (yeast pellets) placed around the periphery of the experimental chamber rather than moving as a group from one yeast pellet to the another. More importantly, insects did not move synchronously from one food choice to another or from the center of the experimental chamber to the periphery.

Factors affecting collembolan grazing preference do not appear to be taxonomically based at the family level. *G. otthii*, one of the most preferred fungal species, is in the same family as *M. tuberiformis*, the least preferred fungal species considered in this study. Similarly, in the first experiment, *Rhizopogon* species tended to be preferred and *Suillus* species tended to be avoided despite being closely related (R. FOGEL pers. comm.).

This study corroborates work conducted by SHAW (1985, 1988). In his studies *O. armatus* preference did not appear to be taxonomically based. The most preferred fungus, *L. rufus* and the third most preferred fungus, *L. proxima* were in the same family as the second least preferred fungus, *Hebeloma crustuliniforme*. Two fungal species were common to both our experiments, *Paxillus involutus* and *H. crustuliniforme*. In SHAW's study *O. armatus* preferred *P. involutus* over *H. crustuliniforme*. Although there was no significant difference between these two species in this study, *F. candida* visited *P. involutus* more often than *H. crustuliniforme* in Experiment 1, the difference might prove to be significant if the fungi were pairwise compared. These studies suggest a common grazing preference across these three collembolan species.

However, these preferences may depend upon the substrate on which the fungi are growing. LEONARD (1984) found that grazing choice was greatly affected by the substrate on which the fungi were growing to the extent that grazing preference changed depending on which substrate the fungi were grown. Collembola grazing choices in nature will be affected by the properties of the species of fungus they encounter as well as the substrate upon which the fungus is growing. In the case of these fungi the mycorrhizal host plant is likely to affect insect preference.

5. Acknowledgements

I would like to thank my advisors Dr. ROBERT FOGEL, Dr. CATHERINE BACH and Dr. BARRY O'CONNOR whose advice greatly assisted me both in my thesis work and in the preparation of this manuscript. I would also like to thank JOHN LUSSENHOP for providing me with cultures of *F. candida* and *P. minuta*.

I would like to thank the administration of University of Michigan Biology Station for its financial support through the Naturalists and Ecologists Training Program funded by the Mellon Foundation and their continued support of my work the following summer through a research assistantship. This work was done in partial fulfillment of the requirements of a Master of Science degree at the University of Michigan.

6. References

ANDERSON, J. M., I. N. HEALEY, 1972. Seasonal and interspecific variation in major components of the gut contents of some woodland Collembola. *Journal of Animal Ecology* **41**, 359–368.

COCHRAN, W. G., G. M. COX, 1957. *Experimental Designs*. 2nd Ed. John Wiley, New York.

FINLAY, R. D., 1985. Interactions between soil micro-arthropods and endomycorrhizal associations of higher plants. *In: FITTER et al. (1985)*.

FITTER, A. H., D. ATKINSON, D. J. READ & M. B. USHER (eds), 1985. *Ecological interactions in soil. Special Publications Series of the British Ecological Society No. 4*. London.

KNIGHT, C. B. & R. A. ANGEL, 1967. A preliminary study of the dietary requirements of *Tomocerus* (Collembola). *American Midland Naturalist* **77**, 511–517.

LEONARD, M. A., 1984. Observations on the influence of culture conditions of the fungal feeding preferences of *Folsomia candida* (Collembola; Isotomidae). *Pedobiologia* **26**, 361–367.

— & P. C. BRADBURY, 1984. Aggregation behaviour in *Folsomia candida* (Collembola: Isotomidae), with respect to previous conditioning. *Pedobiologia* **26**, 369–372.

McMILLAN, J. H., 1976. Laboratory observations on food preference of *Onychiurus armatus* (TULLB.) GISIN (Collembola, Family Onychiuridae). *Revue d'Ecologie et de Biologie du Sol* **13**, 353–364.

MITCHELL, M. J., & D. PARKINSON, 1976. Fungal feeding of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. *Ecology* **57**, 303–312.

MOORE, J. C., E. R. INGHAM, & D. C. COLEMAN, 1987. Inter and intraspecific feeding selectivity of *Folsomia candida* (WILLEM) (Collembola, Isotomidae) on fungi. *Biology and Fertility of Soils* **5**, 6–12.

—, T. V. ST. JOHN & D. C. COLEMAN, 1985. Ingestion of vesicular-arbuscular mycorrhizal hyphae and spores by soil microarthropods. *Ecology* **66**, 1979–1981.

NEWELL, K., 1984. Interaction between two decomposer basidiomycetes and a collembolan under Sitka Spruce: distribution, abundance and selective grazing. *Soil Biology and Biochemistry* **16**, 227–233.

— 1984. Interaction between two decomposer basidiomycetes and a collembolan under Sitka Spruce: grazing and its potential effects of fungal distribution and litter decomposition. *Soil Biology and Biochemistry* **16**, 235–239.

POOLE, T. B., 1959. Studies on the food of Collembola in a Douglas-fir plantation. *Proceedings of the Zoological Society of London* **132**, 71–82.

SHAW, P. J. A., 1985. Grazing preferences of *Onychiurus armatus* (Insecta: Collembola) for mycorrhiza and saprophytic fungi of pine plantations. *In: FITTER et al. (1985)*.

— 1988. A consistent hierarchy in the fungal feeding preferences of the Collembola *Onchiurus armatus*. *Pedobiologia* **31**, 179–187.

STEVENS, R. B., 1974. *Mycology Guidebook*. University of Washington Press, Seattle.

SUTHERLAND, J. R., & J. A. FORTIN., 1968. Effect of nematode *Aphelenchus avenae* on some ectotrophic mycorrhizal fungi and on a red pine mycorrhizal relationship. *Phytopathology* **58**, 519–523.

USHER, M. B., & M. HIDER. 1975. Studies on populations of *Folsomia candida* (Insecta: Collembola); causes of aggregations. *Pedobiologia* **15**, 276–283.

— & C. F. STONEMAN, 1977. *Folsomia candida* – An ideal organism for population studies in the laboratory. *Journal of Biological Education* **11**, 83–90.

VISSEER, S., 1985. Role of the soil invertebrates in determining the composition of soil microbial communities. *In: FITTER et al. (1985)*.

WALTER, D. C., R. A. HUDGENS & D. W. FRECKMAN, 1986. Consumption of nematodes by fungivorous mites, *Tyrophagus spp.* (Acarina: Astigmata: Acaridae). *Oecologia* **70**, 357–361.

WARNOCK, A. J., A. H. FITTER & M. B. USHER, 1982. The influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal association of leek *Allium porrum* and the vesicular-arbuscular mycorrhizal endophyte, *Glomus fasciculatus*. *New Phytologist* **90**, 285–293.

WILKINSON, L., 1987. Systat: The system for statistics. Evanston II: Systat, Inc.

WINER, B. J., 1971. Statistical principles in experimental design, 2nd. ed. New York: McGraw-Hill.

Synopsis: Original scientific paper

SCHULTZ, PEGGY ANN, 1991. Grazing preferences of two collembolan species, *Folsomia candida* and *Proisotoma minuta*, for ectomycorrhizal fungi. *Pedobiologia* **35**, 313–325.

Folsomia candida (WILLEM) and *Proisotoma minuta* (TULLBERG) reared in the laboratory preferentially grazed ectomycorrhizal fungi growing on nutrient agar. *F. candida*'s preferences for fifteen ectomycorrhizal fungi were initially tested using a 4×4 balanced lattice experimental design. *Leccinum scabrum*, the most visited fungus and *Melanogaster tuberiformis*, the least visited fungus were the only choices that differed significantly in visitation by *F. candida*. Pairwise comparisons of preferred and less preferred fungi were performed with both *F. candida* and *P. minuta*. In the pairwise comparisons with *F. candida* and *P. minuta*, *Gautieria otthii* was preferred over *L. scabrum*, *Alpova olivaceotinctus* or *M. tuberiformis*. *P. minuta* preferred *L. scabrum* over *A. olivaceotinctus* and *M. tuberiformis*. *P. minuta* and preferred non-inoculated control plugs over *A. olivaceotinctus* and *M. tuberiformis*. Fungal preference did not appear to be taxonomically based at the family level and did not appear to be related to morphology.

Key words: Collembola, grazing preference, *Folsomia candida*, *Proisotoma minuta*, ectomycorrhizal fungi, *Leccinum scabrum*, *Melanogaster tuberiformis*, *Alpova olivaceotinctus*, or *Gautieria otthii*.

Address of the authoress: Department of Botany, Duke University, Durham, N.C. 27706, U.S.A.